RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SHORT COMMUNICATION

# Large canopy and animal-dispersed species facilitate natural regeneration in tropical forest restoration

Lara M. Mendes[1], Ricardo G. César[2,3], Alexandre Uezu[1], Tiago P. Beltrame[1], Luiz C. E. Rodriguez[2], Haroldo B. Gomes[1], Laury Cullen[1]

**Realizing the benefits of forest restoration requires that these ecosystems be maintained after the senescence of planted trees through facilitation of natural regeneration. We analyzed the effect of tree canopy cover, dispersal syndrome, deciduousness, and taxon in facilitating natural regeneration in tropical forest restoration planting. Canopy cover had additive positive effect on natural regeneration when combined with animal dispersal or evergreen trees. Animal dispersal had a positive effect on facilitating natural regeneration abundance, while evergreen species had a positive effect on natural regeneration richness only. Although variation within and among species was high, restoration practitioners could consider using species with these traits to facilitate natural regeneration and hence development of restoration plantings.**

**Key words: Atlantic Forest, deciduousness, ecological restoration, recruitment, species selection**

### Implications for Practice

- We provide a ranking of species with the potential to facilitate natural regeneration in the Atlantic Forest.
- Canopy cover alone is not a good predictor of facilitation potential of planted native trees.
- Animal-dispersed and evergreen trees with large canopy show potential to facilitate natural regeneration in the Atlantic Forest.

## Introduction

Ecological restoration has become a global movement justified by its key ecological services, such as climate change mitigation and habitat provision (Mansourian & Vallauri 2014), further strengthened by the UN declaration of the Decade on Ecosystem Restoration from 2021 to 2030. Since several positive outcomes of native species plantings can take decades to manifest, it is key that these ecosystems persist through time, otherwise human and financial resources may be lost (Garcia et al. 2016). Natural regeneration of native trees (i.e. the process of spontaneous establishment of seedlings; Chazdon 2014) confers the resilience needed for restoration plantings to persist through time (Chazdon & Guariguata 2016).

Persistence of ecosystems under restoration is challenging because drivers of degradation are sometimes beyond practitioners' control (Reid et al. 2017). Alternatively, other drivers of restoration fate, such as planted species composition and traits, can be more easily manipulated in restoration projects and influence restoration success (Fink et al. 2009; Martínez-Garza et al. 2013; Schweizer et al. 2015; Holl et al. 2020). Planted species' traits affect light interception (Almeida & Viani 2019), native tree recruitment and development (De Pena-Domene et al. 2016; Galindo et al. 2017; Li et al. 2018), seed dispersal visitation (Fink et al. 2009), and community resilience (Timpane-Padgham et al. 2017). In other words, the differential structure and resources provided by the diverse species planted will affect the dispersal limitation, composition, abundance, and diversity of the natural regeneration (Li et al. 2018; Camargo et al. 2020), which in turn will affect ecological processes (Lanuza et al. 2018) and future forest composition.

Different tree traits may interact to influence natural regeneration (Martínez-Garza et al. 2013), in addition to the effect of landscape context (Charles et al. 2016). Therefore, surveys that control for landscape effect and include multiple traits must be considered to identify species that foster natural regeneration in restoration plantings. Here, we sampled 360 trees of 24 species to analyze their traits (canopy cover, dispersal syndrome, and deciduousness) that facilitate abundance and richness of spontaneously regenerating tree seedlings (hereafter regenerating

Author contributions: LMM, AU, LC conceptualized this research; LMM, AU, TPB, LC developed the methodology; LMM, HBG gathered the data; LMM, RGC, AU analyzed the data; LMM, AU, RGC, LC wrote and reviewed the manuscript; all steps were supervised by TPB, LCER, LC.

[1]Ecological Research Institute (IPE), Dom Pedro I Highway, km 47, 12960-000, Nazaré Paulista, SP, Brazil
[2]Department of Forestry Sciences, University of São Paulo, ESALQ, Av. Pádua Dias, 11, 13418-900, Piracicaba, SP, Brazil
[3]Address correspondence to R. G. César, email ricardogoce123@gmail.com


doi: 10.1111/rec.13406
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13406/suppinfo

seedlings) in restoration plantings. We hypothesized that: (1) animal-dispersed trees or larger canopy trees are more likely to attract seed dispersers and provide environmental conditions to facilitate establishment of regenerating seedlings in restoration sites, since canopy cover is related to planted trees' potential to suppress shade-intolerant invasive grasses that hinder restoration plantings in the region (Galindo et al. 2017); (2) deciduous trees may have an overall negative or neutral effect on regenerating seedlings, as the seasonal gap created by deciduousness will provide more light for seedlings (Gandolfi et al. 2007), while it may increase the hydrological stress due to increased temperature in the dry season when compared to evergreen trees.

## Methods

### Study Site

This study was carried out in restoration plantings in the western part of São Paulo State, Southeast Brazil, in the Pontal do Paranapanema region. Mean annual precipitation in the region is 1,341 mm and mean annual temperature is 24.1°C, with wet summers and dry winters. Forest cover in the region is composed of seasonal deciduous forests of the Atlantic Forest biome, one of the most diverse and threatened biodiversity hotspots of the world (Laurance 2009). The study region is plain, with elevation varying from 265 to 320 m a.s.l. and predominant soil classes in the region are Ferrasols and Ultisols. The study landscape has only 18% native forest cover embedded in agricultural landscapes (Uezu & Metzger 2016).

We gathered data from 7-year-old restoration plantings summing 75 ha carried out by planting 2,000 trees/ha of approximately 40 species. The framework planting method was applied, in which fast-growing species are alternated with slow-growing species to accelerate the development of forest structure while maintaining high species richness (Rodrigues et al. 2009). Invasive grasses were suppressed using herbicides before planting and every 3 months for the following 2 years after planting. No soil fertilization was carried out. Finally, the area was protected from cattle by fencing and from fire by firebreaks (Fig. 1).

### Data Gathering

We measured planted tree traits and regenerating seedlings under individual trees in the restoration planting. We selected 24 species with the largest mean diameter at breast height and height from the dataset of Amaral (2017) from these plantings, and measured canopy cover and abundance and richness of regenerating seedlings beneath 15 trees of each of the 24 species selected. We selected trees by dividing the 75-ha restoration planting into 15 areas of equal size and sampling one tree of each species in each area, with a minimum distance of 50 m between

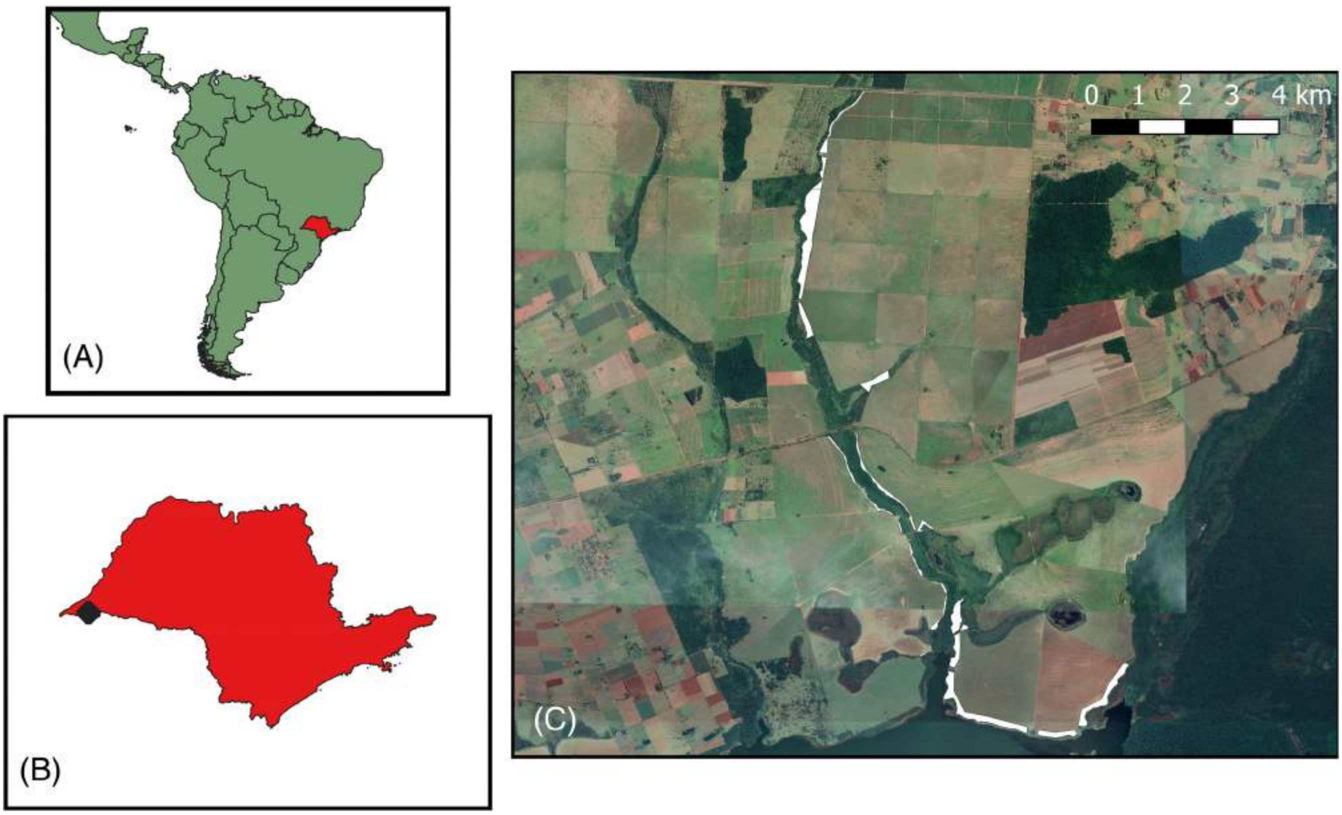


Figure 1. Location of the 7-year-old Atlantic Forest restoration plantings where trees were sampled. (A) Location in Latin America, (B) location in São Paulo State, Brazil, (C) plantings are highlighted in white in the Pontal do Paranapanema region.

trees of the same species. By distributing tree sampling equally among areas, we controlled landscape effects (i.e. distance from forest remnants) on regenerating seedlings. If a particular species was not found in one of the areas, we would sample an additional tree in the next area, always keeping the minimum 50 m distance. We sampled a total of 360 trees and classified all according to dispersal syndrome (animal or nonanimal dispersed) and deciduousness (deciduous or evergreen, Table 1).

For each tree sampled, we measured canopy cover as the area of the circle for which the diameter was the average of the longest and shortest extents of the projection of the tree canopy on the ground. For abundance and richness of regenerating seedlings, we established a 10 $m^2$ circle around the planted tree and counted and separated into morphospecies all regenerating seedlings with height greater than 0.5 m.

### Data Analysis

We ranked planted species based on their combined performance for canopy cover and abundance and richness of regenerating seedlings. Species in which the mean value for a given indicator falls within one SE interval for the best-ranked species for that indicator belong to group 1. The first species in which the mean falls outside the interval of the first ranked species will serve as the baseline for group 2, and so forth. Since the number of ranks varied for each indicator, we normalized rank position to range from 0 to 1 by dividing species rank by the total number of ranks for that indicator.

To identify traits that could benefit regenerating seedlings, we developed negative binomial generalized linear models for abundance and richness of regenerating seedlings based on the following parameters: species, dispersal syndrome, deciduousness, and tree canopy cover. We used the *glm.nb* function in R software (Team RC 2018; Ripley et al. 2020). We generated all models possible with these parameters plus a null model and compared them using the corrected Akaike information criteria (AICc) and calculated the relative importance of the parameters among the best models ($\Delta$AICc <2) by the relative weight of the models that contained the parameters.

## Results

Native tree species sampled varied in canopy cover and regenerating seedlings among and within species (Table 1). While the top-ranked species vary regarding dispersal syndrome and deciduousness, all of them have large mean canopy (Table 1 and Fig. 2). Further details on rankings can be found in Appendix S1.

Canopy cover was in most of the best models for regenerating seedlings' abundance ($\Delta$AICc 0.00, 0.97, 1.91) and species richness ($\Delta$AICc 0.0, 0.66, and 1.97), but alone it was not a good

**Table 1.** Species traits for the tree species sampled in restoration plantings in the Pontal do Paranapanema region. CBH, circumference at breast height; Canopy cover, area of the canopy projection; NR, natural regeneration; Dispersal, prevalent seed dispersal syndrome of the species; Deciduousness, seasonality of leaf loss of the species, divided in two groups: deciduous: loses half or more of the leaves once a year and evergreen: maintains canopy cover all year round; Rank, final position on the ranking considering canopy size and regenerating seedlings' abundance and richness under planted trees, ranking details can be found in Supplement 1.

| *Species* | *CBH (cm)* | *Canopy Cover ($m^2$)* | *NR Abundance* | *NR Richness* | *Dispersal* | *Deciduousness* | *Rank* |
|---|---|---|---|---|---|---|---|
| *Trema micrantha* (L.) Blume | 53.4 ± 7.6 | 27.5 ± 10.3 | 6.5 ± 7.7 | 2.3 ± 1.7 | Animal | Deciduous | 0.8 |
| *Senegalia polyphylla* (DC.) Britton & Rose | 35.8 ± 5 | 40.6 ± 14.9 | 5.1 ± 6.6 | 2.2 ± 2.4 | Abiotic | Deciduous | 0.9 |
| *Croton urucurana* Baill. | 36.9 ± 6.2 | 30.9 ± 8.8 | 4.3 ± 7.1 | 1.9 ± 2.4 | Abiotic | Deciduous | 1.0 |
| *Inga sessilis* (Vell.) Mart. | 34.6 ± 5.4 | 29.8 ± 7.4 | 4.1 ± 5.4 | 1.8 ± 1.8 | Animal | Evergreen | 1.0 |
| *Plinia rivularis* (Cambess.) Rotman | 37.8 ± 7.4 | 25.9 ± 7.6 | 4.3 ± 6.6 | 2.3 ± 2.8 | Animal | Evergreen | 1.2 |
| *Ceiba speciosa* (A.St.-Hil.) Ravenna | 34.5 ± 15.9 | 18 ± 9.7 | 6.2 ± 7.4 | 1.9 ± 1.8 | Abiotic | Deciduous | 1.2 |
| *Peltophorum dubium* (Spreng.) Taub. | 35.1 ± 7.9 | 19.7 ± 4.9 | 8.9 ± 12.2 | 2.3 ± 2.7 | Abiotic | Deciduous | 1.2 |
| *Croton floribundus* Spreng. | 30.1 ± 3.1 | 31 ± 11.5 | 3.3 ± 5.9 | 1.5 ± 1.8 | Abiotic | Deciduous | 1.3 |
| *Anadenanthera colubrina* var. *cebil* (Griseb.) Altschul | 40.8 ± 7.6 | 21 ± 4.7 | 4.5 ± 7.6 | 1.8 ± 2.5 | Abiotic | Deciduous | 1.3 |
| *Jacaratia spinosa* (Aubli) A. DC. | 51.6 ± 10.3 | 12.6 ± 4.1 | 8.8 ± 11 | 2.3 ± 1.8 | Animal | Deciduous | 1.4 |
| *Poecilanthe parviflora* Benth. | 17 ± 4.8 | 15.8 ± 7.3 | 5.5 ± 8.8 | 1.9 ± 1.9 | Abiotic | Evergreen | 1.4 |
| *Sapium haematospermum* Mll. Arg. | 20.1 ± 5.8 | 9.3 ± 3.4 | 5.5 ± 8.7 | 2.1 ± 2.6 | Animal | Evergreen | 1.5 |
| *Gochnatia polymorpha* (Less.) Cabrera | 19.4 ± 5.3 | 13.7 ± 5.4 | 5 ± 4.8 | 1.9 ± 1.4 | Abiotic | Deciduous | 1.6 |
| *Mabea fistulifera* Mart. | 29.5 ± 7.1 | 17.7 ± 5 | 3.9 ± 6.2 | 1.6 ± 2.4 | Animal | Deciduous | 1.7 |
| *Pradosia lactescens* (Vell.) Radlk. | 24.9 ± 4.6 | 10.6 ± 2.5 | 4.7 ± 6.7 | 1.7 ± 1.9 | Animal | Evergreen | 1.8 |
| *Anadenanthera colubrina* (Vell.) Brenan | 28.6 ± 7.6 | 27.3 ± 12 | 1.9 ± 4 | 1.1 ± 1.9 | Abiotic | Deciduous | 1.8 |
| *Aspidosperma parvifolium* A.DC. | 27.2 ± 7.7 | 14.7 ± 6 | 3.7 ± 4.1 | 1.7 ± 1.5 | Abiotic | Deciduous | 1.9 |
| *Alchornea glandulosa* Poepp. | 21.4 ± 3.6 | 10.5 ± 3.2 | 4.8 ± 8.2 | 1.5 ± 1.6 | Animal | Evergreen | 2.0 |
| *Astronium graveolens* Jacq. | 26.4 ± 4.4 | 11.8 ± 3.1 | 4.5 ± 9.8 | 1.2 ± 2 | Abiotic | Deciduous | 2.0 |
| *Triplaris americana* L. | 26.3 ± 9.2 | 10.4 ± 7.7 | 3.3 ± 4.5 | 1.5 ± 1.4 | Abiotic | Evergreen | 2.0 |
| *Cecropia pachystachya* Trécul | 38.6 ± 5.3 | 16.8 ± 5.6 | 2.5 ± 5.5 | 0.9 ± 1.3 | Animal | Evergreen | 2.2 |
| *Pouteria ramiflora* (Mart.) Radlk. | 14.1 ± 2.3 | 10 ± 4 | 2.9 ± 5 | 0.8 ± 1.1 | Animal | Deciduous | 2.5 |
| *Handroanthus serratifolius* (Vahl) S.O.Grose | 19.6 ± 3.8 | 11.2 ± 2.5 | 1.5 ± 2.9 | 1.1 ± 1.7 | Abiotic | Deciduous | 2.8 |
| *Lonchocarpus muehlbergianus* Hassl. | 23.6 ± 6.4 | 13.9 ± 5.6 | 1.1 ± 2 | 0.7 ± 1.2 | Abiotic | Deciduous | 2.9 |

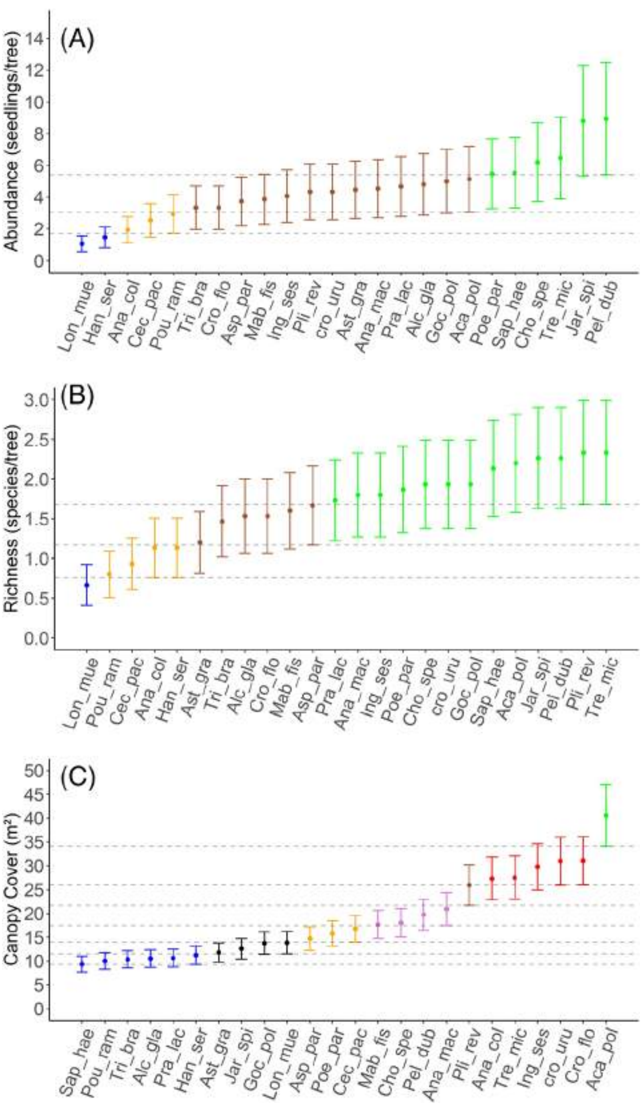


Figure 2. Natural regeneration (A) abundance and (B) species richness and (C) canopy cover for the 24 species sampled in 7-year-old forest restoration plantings in the Atlantic Forest of the Pontal do Paranapanema region, Brazil. Values are shown as means ± 1 SE and *n* = 15 for each species. Species names are represented by the first three letters of the genus and species name (see Table 1 for full species names). Dashed lines separate the ranking groups for each attribute measured, separated by colors. Species in which the mean value for a given indicator falls within 1 SE interval for the best-ranked species for that indicator belong to the first group; the first species in which the mean falls outside the standard error interval of the first ranked species will serve as the baseline for group 2, and so forth.

predictor of regenerating seedlings, thus its additive effect with animal dispersal and deciduousness is more determinant for regenerating seedlings (Fig. 3, Appendix S2). While canopy cover and animal dispersion were similarly important for regenerating seedlings' abundance, canopy cover and deciduousness were important for species richness of regenerating seedlings (Table 2). Planted tree species was not a good predictor of natural regeneration, being included only in models $\Delta$AICc > 24 and 36 for regenerating seedlings' abundance and species richness, respectively (Tables S2, S3, and S4). Although model selection indicated species traits that benefit spontaneous regeneration, the error of predicted values of these models overlap (Fig. 3), and further studies are required to predict the effect of tree traits on natural regeneration.

## Discussion

While other studies have separately approached the role of dispersal syndrome (e.g. Viani et al. 2015), deciduousness (Gandolfi et al. 2009), and canopy size and light interception (Almeida & Viani 2019) and species composition (Gómez-Aparicio et al. 2005), our study is one of the few in identifying their simultaneous role in facilitating natural regeneration. Canopy cover had an additive effect with animal dispersal and deciduousness for facilitating regenerating seedlings, but it is a poor predictor by itself (e.g. Almeida & Viani 2019). Even though species varied significantly in abundance and richness of regenerating seedlings under their canopy, species traits were a better predictor of regenerating seedlings than taxon. Species traits are also a better predictor of the microclimatic conditions under the canopy, e.g. tree height and height of branching are closely related light interception, as observed by Almeida and Viani (2019).

Animal-dispersed species attract fauna that will bring other animal-dispersed seeds to restoration sites, creating a positive feedback that contributes to forest persistence (Lameira et al. 2019). Most of the 24 species surveyed are already producing fruits, therefore increased abundance and richness of regenerating seedlings were expected under animal-dispersed trees, such as *Trema micrantha* (nettle tree). Avendaño-Yáñez et al. (2014) also observed that *T. micrantha* reduced the mortality of planted seedlings below its canopy, while seedling growth was not hindered by the shading; not surprisingly, this species was one of the best ranked in our study.

We recognize that both seed dispersers and regenerating seedlings may be affected not only by the traits of the tree sampled, but also by surrounding trees and environmental conditions. For example, bird visitation, seed rain, and natural regeneration are influenced by the size of tree clusters, as well as canopy cover, and not only by traits of a single tree (Fink et al. 2009; Robinson 2010; Zahawi et al. 2013). For example, Zahawi et al. (2013) observed that large tree clusters (144 $m^2$) had more seedlings established than smaller clusters (16 $m^2$) indicating the importance of the joint canopy cover of several trees to facilitate recruitment in tropical forests under restoration. However, given that some species—such as *T. micrantha*, *Senegalia polyphylla*, and *Peltophorum dubium*—have consistently showed high regenerating seedlings' abundance, richness, and canopy cover, we believe that our results represent the traits of the trees sampled, despite surrounding noise.

Canopy cover can create microclimatic conditions that benefit seedling development, as well as being a key indicator of success in forest restoration (Holl et al. 2018). The effect of tree canopy on microclimate is influenced both by individual

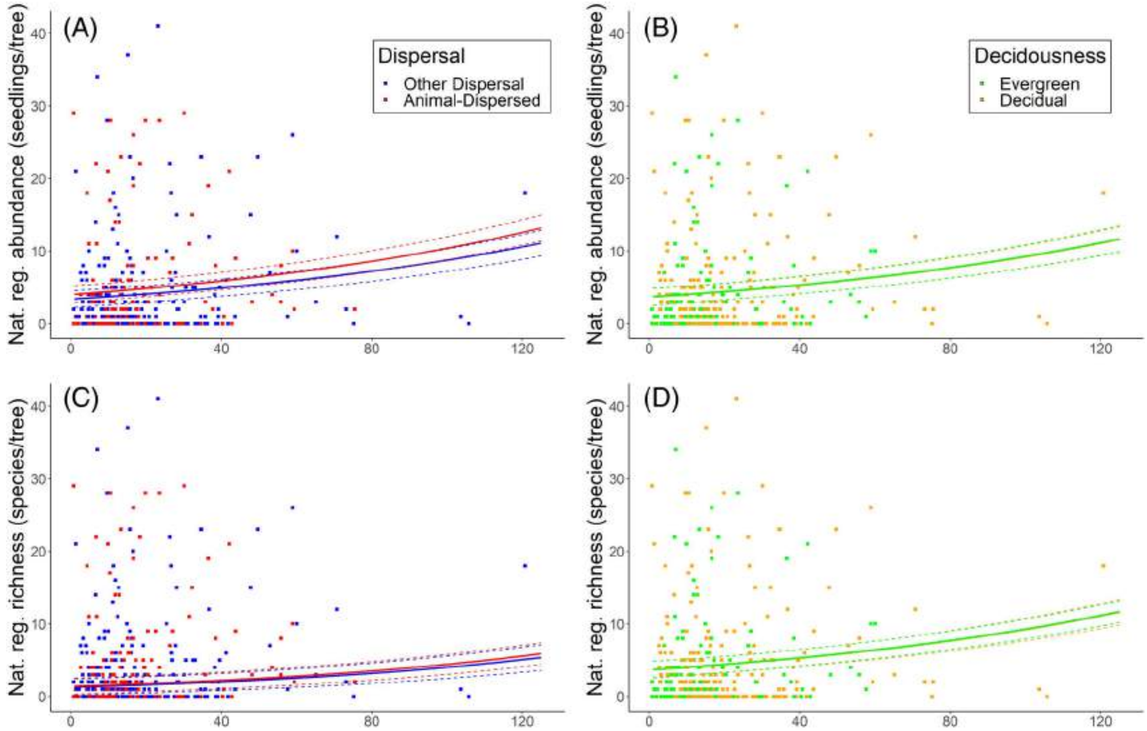


Figure 3. Natural regeneration under planted trees in 7-year-old native tree restoration plantings in the seasonal Atlantic Forest, Brazil. Upper graphs represent abundance of natural regeneration for planted tree canopy cover and (A) dispersal syndrome, (B) tree deciduousness. Lower graphs represent species richness of natural regeneration for (C) dispersal syndrome, (D) tree deciduousness. Lines are predicted values for the models generated for canopy cover and tree traits (Table 1 and Appendix S2).

**Table 2.** Relative importance of the parameters to estimate abundance and species richness of natural regeneration under trees planted in restoration plantings of the Atlantic Forest in the Pontal do Paranapema region, Brazil. Relative importance is calculated only for models ΔAICc <2.

| *Parameter* | *Importance* | *Models Included* |
|---|---|---|
| Abundance of natural regeneration | | |
| Canopy cover | 69% | 3 |
| Dispersal | 66% | 3 |
| Deciduousness | 47% | 3 |
| Species richness of natural regeneration | | |
| Canopy cover | 100% | 3 |
| Dispersal | 66% | 2 |
| Deciduousness | 52% | 2 |

characteristics, such as tree height and crown format (Almeida & Viani 2019), as well as species traits, such as leaf specific area, deciduousness, and leaf area index (Gandolfi et al. 2009). The shading of evergreen trees may favor the development of more diverse taxa under their canopy, probably reducing water stress compared to deciduous trees that lose leaves during the dry season (Gandolfi et al. 2009).

Other authors also observed that increased canopy cover favored natural regeneration and growth in Mediterranean (Gómez-Aparicio et al. 2005) and Andean riparian forests (Galindo et al. 2017) as well as forest restoration plantings (Zahawi et al. 2013). While trees with larger canopy cover had increased abundance and richness of regenerating seedlings under them, the best models for regenerating seedlings included the combined effect of canopy cover plus animal dispersal or deciduousness, corroborating that the area covered by tree canopy may be a useful trait, but its effect is related to other tree traits (Almeida & Viani 2019).

While we are not advocating for reducing trait diversity in restoration plantings, or that species selection alone will decide the fate of planted forests, tropical forest restoration could benefit from a range of species with complementary traits to facilitate natural regeneration and contribute to forest longevity in the long term. Around 50% of the trees planted for forest restoration in the Atlantic Forest are selected for quickly developing a canopy and creating a microclimate that shades out invasive grasses and facilitates regeneration (Rodrigues et al. 2009); selecting animal-dispersed species in this group could further improve the potential of these species to facilitate natural regeneration in restoration plantings. Finally, the restoration supply chain and policies could foment the use of such species, as the species with more abundance and richness of regenerating seedlings (e.g. *T. micrantha*, *S. polyphylla*, *Croton urucurana*, *Inga sessilis*, see Table 1 for more) are abundantly produced in seedling nurseries (Vidal et al. 2020) and recommended for restoration plantings in the region (Barbosa et al. 2017).

## Acknowledgments

The authors are thankful to the "Morro do Diabo" State Park staff for housing and to Cecilia Dante for the support during the field work. The authors have no conflict of interest to declare.

## LITERATURE CITED

Almeida C, Viani RAG (2019) Selection of shade trees in forest restoration plantings should not be based on crown tree architecture alone. Restoration Ecology 27:832–839

Amaral LGC (2017) Aboveground carbon increment stored on the aerial part of restoration plantings in corridors integrating conservation units and riparian fragments. University of São Paulo, São Paulo-SP, Brazil.

Avendaño-Yáñez ML, Sánchez-Velásquez LR, Meave JA, Pineda-López M del R (2014) Is facilitation a promising strategy for cloud forest restoration? Forest Ecology and Management 329:328–333

Barbosa LM, Shirasuna RT, de Lima FC, Ortiz PRT, Barbosa KC, Barbosa TC (2017) Lista de espécies indicadas para Restauração Ecológica para diversas regiões do Estado de São Paulo. Instituto de Botânica, São Paulo, Brazil

Camargo PHSA, Pizo MA, Brancalion PHS, Carlo TA (2020) Fruit traits of pioneer trees structure seed dispersal across distances on tropical deforested landscapes: implications for restoration. Journal of Applied Ecology 57: 2329–2339

Charles LS, Dwyer JM, Mayfield MM (2016) Rainforest seed rain into abandoned tropical Australian pasture is dependent on adjacent rainforest structure and extent. Austral Ecology 42:238–249.

Chazdon RL (2014) Second-growth: the promise of forest regeneration in the age of degorestation. University of Chicago Press, Chicago, Illinois

Chazdon RL, Guariguata MR (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48: 716–730

De Pena-Domene M, Martinez-garza C, Howe HF (2016) Early recruitment dynamics in tropical restoration. Ecological Applications 23:1124–1134. http://www.jstor.org/stable/23441611

Fink RD, Lindell CA, Morrison EB, Zahawi RA, Holl KD (2009) Patch size and tree species influence the number and duration of bird visits in forest restoration plots in southern Costa Rica. Restoration Ecology 17:479–486

Galindo V, Calle Z, Chará J, Armbrecht I (2017) Facilitation by pioneer shrubs for the ecological restoration of riparian forests in the Central Andes of Colombia. Restoration Ecology 25:731–737

Gandolfi S, Joly CA, Rodrigues RR (2007) Permeability - impermeability: canopy trees as biodiversity filters. Scientia Agricola 64:433–438

Gandolfi S, Joly CA, Leitão Filho H de F (2009) 'Gaps of deciduousness': cyclical gaps in tropical forests. Scientia Agricola 66:280–284

Garcia LC, Hobbs RJ, Ribeiro DB, Tamashiro JY, Santos FAM, Rodrigues RR (2016) Restoration over time: is it possible to restore trees and non-trees in high-diversity forests? Applied Vegetation Science 19:655–666

Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. Journal of Vegetation Science 16:191–198

Holl KD, Reid JL, Oviedo-Brenes F, Kulikowski AJ, Zahawi RA (2018) Rules of thumb for predicting tropical forest recovery. Applied Vegetation Science 21:669–677

Holl KD, Reid JL, Cole RJ, Oviedo-Brenes F, Rosales JA, Zahawi RA (2020) Applied nucleation facilitates tropical forest recovery: lessons learned from a 15-year study. Journal of Applied Ecology 57:2316–2328

Lameira LL, Ferreira FCG, Filardi RAE, Queiroz JM, Sansevero JBB (2019) Plant-canopy effects on natural regeneration in sites under restoration: do tree species matter? Floresta e Ambiente 26:1–8

Lanuza O, Casanoves F, Zahawi RA, Celentano D, Delgado D, Holl KD (2018) Litterfall and nutrient dynamics shift in tropical forest restoration sites after a decade of recovery. Biotropica 50:491–498

Laurance WF (2009) Conserving the hottest of the hotspots. Biological Conservation 142:1137

Li L, Cadotte MW, Martínez-Garza C, de la Peña-Domene M, Du G (2018) Planting accelerates restoration of tropical forest but assembly mechanisms appear insensitive to initial composition. Journal of Applied Ecology 55: 986–996

Mansourian S, Vallauri D (2014) Restoring forest landscapes: important lessons learnt. Environmental Management 53:241–251

Martínez-Garza C, Bongers F, Poorter L (2013) Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? Forest Ecology and Management 303:35–45

Reid JL, Wilson SJ, Bloomfield GS, Cattau ME, Fagan ME, Holl KD, Zahawi RA (2017) How long do restored ecosystems persist. Annals of the Missouri Botanical Garden 102:258–265

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D (2020) Package 'MASS'. https://cran.r-project.org/web/packages/MASS/MASS.pdf

Robinson WD (2010) The challenges of studying vertebrates in habitat treatment plots. Open Environmental Sciences 4:21–23

Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. Biological Conservation 142:1242–1251

Schweizer D, Machado R, Durigan G, Brancalion PHS (2015) Phylogenetic patterns of Atlantic forest restoration communities are mainly driven by stochastic, dispersal related factors. Forest Ecology and Management 354: 300–308

Team RC (2018) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria

Timpane-Padgham BL, Beechie T, Klinger T (2017) A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. PLoS One 12:e0173812

Uezu A, Metzger JP (2016) Time-lag in responses of birds to Atlantic forest fragmentation: restoration opportunity and urgency. PLoS One 11:1–16

Viani RAG, Vidas NB, Pardi MM, Castro DCV, Gusson E, Brancalion PHS (2015) Animal-dispersed pioneer trees enhance the early regeneration in Atlantic Forest restoration plantations. Natureza & Conservação 13:41–46

Vidal CY, Naves RP, Viani RAG, Rodrigues RR (2020) Assessment of the nursery species pool for restoring landscapes in southeastern Brazil. Restoration Ecology 28:427–434

Zahawi RA, Holl KD, Cole RJ, Reid JL (2013) Testing applied nucleation as a strategy to facilitate tropical forest recovery. Journal of Applied Ecology 50:88–96

## Supporting Information

The following information may be found in the online version of this article:

**SUPPLEMENT S1**. Species ranking.
**SUPPLEMENT S2**. Models generated.

*Received: 29 September, 2020; First decision: 4 November, 2020; Revised ; Accepted: 1 April, 2021*

*Coordinating Editor: Leighton Reid*